Morphology, anatomy, and ontogeny in the Asterothyriaceae (Ascomycota: Ostropales), a misunderstood group of lichenized fungi

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Based on morphological, anatomical, and ontogenetical data, the systematics of Asterothyrium, Psorotheciopsis, and Gyalidea (including Solorinella) is revised. The three genera form a natural group for which the name Asterothyriaceae is retained; they share hemiangiocarpous apothecia, true paraphyses, non-amyloid, “annelascaceous” asci, euseptate ascospores, and a chlorococcoid phycobiont. Apothecial ontogeny is characterized by the formation of a covering layer which ruptures during development. Apothecia are sessile (most species of Gyalidea, Psorotheciopsis) or immersed-erumpent with overarching or recurved teeth formed by the covering layer (some species of Gyalidea, Asterothyrium). Flask-shaped, immersed pycnidia (type I) occur in all three genera. Squad-conical pycnidia adnate to the margin of the thallus (type II) were found in Psorotheciopsis and Asterothyrium, while apllanate pycnidia immersed in the thallus centre (type III) are restricted to Asterothyrium. All pycnidial types produce conidia of variable size, shape and septation. Several characters shared by Psorotheciopsis and Asterothyrium, i.e. corticate, whitish thalli, pigmented and/or immersed-erumpent apothecia, large and thick-walled ascospores, and frequent formation of pycnidia, are possibly adaptations to their preferred habitat: canopy leaves in the tropical rain forests. The closest relative of the Asterothyriaceae is Gyalideopsis in the Gomphillaceae. It agrees in most aspects with Gyalidea, but differs by its anastomosing paraphysoids and hyphophorous conidiomata. Both families are placed in Ostropales, sharing hemiangularicarpous apothecia, non-amyloid asci, and “annelasaceous” ascus type, with the Stictidaceae, Odontotremataceae, Thelotremataceae, and Graphidaceae.

Key words: Asterothyrium, Gomphillaceae, Gyalidea, Gyalideopsis, lichen, Psorotheciopsis, Solorinella, taxonomy
Introduction

In his monograph of foliicolous lichens, Santesson (1952: p. 331) wrote about Psorotheciopsis Rehm: “The lichens of this genus have been stumbling-blocks for mycologists.” Indeed, the three species recognized by him do have three generic synonyms and were referred to ten further genera of lichenized and non-lichenized fungi (Table 1). Psorotheciopsis itself was assigned to families such as the operculate Pezizaceae and Megalosporaceae in the Lecanorales (Table 2).

A similar situation is found in Asterothyrium Müll. Arg.: the ten species listed in Santesson (including A. rotuliforme (Müll. Arg.) Sérus. and A. umbilicatum (Müll. Arg.) Müll. Arg.; see Sérusiaux & de Sloover 1986, Lücking et al. 1998) have seven generic synonyms (two of them invalid) and were partly referred to further 12 genera of lichenized and non-lichenized fungi (Table 1). Asterothyrium itself was included in the Patellariaceae and Thelotremataceae, among other families (Table 2).

The Asterothyriaceae are based on Vainio’s (1896) and Zahlbruckner’s (1905) Ectolechiaceae, which included Asterothyrium, Tricharia Fée, Echinoplaca Fée, Actinoplaca Müll. Arg.,...
Sporopodium Mont., and Byssolecania Vain., among others. When first introducing the name Asterothyriaceae, Watson (1929) retained Asterothyrium, Byssolecania, and Actinoplaca, still a highly heterogeneous assemblage. Santesson (1952) recognized six genera as being related: Asterothyrium, Psorotheciospis, Calenia Müll. Arg., Gyalectidium Müll. Arg., Echinoplaca (including Actinoplaca), and Tricharia. This group largely corresponds to Ectolechiaceae sensu Vainio and Zahlbruckner, but since the type genus, Sporopodium, had to be referred to the Lecanorales, Santesson adopted the name Asterothyriaceae.

Vezda (1979) presented the first modern treatment of the family, adding Gyalidea Lett. (Vezda 1966, Lumbsch et al. 1991), Solorinella Anzi (Poelt & Vezda 1969), Gyalideaopsis Vezda (Vezda 1972, Lumbsch & Hawksworth 1987), Gomphillus Nyl., and Aulaxina Fée. Linhartia was segregated from Psorotheciospis, and the latter, on account of its large, thick-walled ascospores, was referred to the Megalosporaceae (Vezda 1973) and, more recently, to the Gomphillaceae (Eriksson & Hawksworth 1987, 1993). Vezda (1979) recognized two entities within the Asterothyriaceae: one with branched and anastomosing paraphyses and hyphophorous conidiomata (Vezda 1973), and a one with unbranched paraphyses and pycnidial conidiomata, including Asterothyrium, Gyalidea, Linhartia, and Solorinella. After segregating the taxa producing hyphophores in a separate family Gomphillaceae (Vezda & Poelt 1987), the remaining four genera were retained as Asterothyriaceae s.stricto (Eriksson & Hawksworth 1987).

However, Vezda and Poelt (1987) considered Asterothyrium to take an isolated position, although they gave no reasons for their view, and later assigned Gyalidea, Linhartia, and Solorinella to a new family Solorinellaceae (Vezda & Poelt 1987). Asterothyrium, the only genus left in the Asterothyriaceae, was then compared to Chroodiscus (Müll. Arg.) Müll. Arg. and eventually referred to the Thelotremataceae (Vezda 1979, Vezda & Poelt 1987, Eriksson & Hawksworth 1993, Hawksworth & Eriksson 1994, Aptroot in Aptroot et al., 1994), and the Asterothyriaceae temporarily “disappeared” into oblivion.

This view was partly confirmed by a preliminary phylogenetic study of the group performed by Dennetièr and Péroni (1998), analyzing 15 characters in 15 taxa. Psorotheciospis premnella fell in a clade with Linhartia, while Asterothyrium merged with Graphidaceae and Thelotremataceae. However, performing a more detailed analysis of 31 characters in 24 taxa, Lücking (1999) found that Asterothyriaceae sensu Eriksson and Hawksworth (1987) and Gomphillaceae sensu Vezda and Poelt (1987) form coherent groups related to Thelotremataceae and Graphidaceae in the Ostropales. He therefore reinstated Asterothyriaceae sensu Eriksson and Hawksworth (1987), placing Solorinellaceae in synonymy. Based on another analysis, using 125 phenotype characters in 24 species, and following earlier observations made by Aptroot and Sipman (1991), Aptroot and Lücking (2002) merged Solorinella with Gyalidea, leaving the Asterothyriaceae with three genera.

In this paper, we present data on the apothecial morphology, anatomy and ontogeny of Gyalidea (including Solorinella), Psorotheciospis, and Asterothyrium, in order to test our view of this group as a natural entity and to study the relationships between the different genera and species.

Material and methods

The following taxa were used for morphological, anatomical, and ontogenetic studies:


Brazil, Puiggar 1748 (G, holotype).

Asterothyrium aspidospermatis (Peres) Lücking & Séns.: Brazil, Heringer s.n. (URM 72025).

Asterothyrium atromarginatum Herrera-Campos & Lücking: Mexico, Herrera-Campos et al. s.n. (MEXU, holotype).


Asterothyrium chroodisciforme Lücking: Costa Rica, Lücking 91-4014, 91-6000 (both hb. Lücking).

Peru, Santesson & Santesson s.n. (UPS).
Asterothyrium decipiens (Rehm) R.Sant. (type species of Stictocyclusiophyllum) **Brazil. Ule 1238 (UPS, isotype of Stictocyclusiophyllum decipiens Rehm).**

Philippines, **Elmer 14493c (B).**


Asterothyrium hedbergii Kalb & Vobis: Brazil, Kalb s.n. (hb. Kalb, holotype).

Asterothyrium leptoosphorum Müll.Arg.: **Costa Rica, Pittier 5111 (G, holotype).**

Asterothyrium hedbergii Kalb & Vobis: Brazil, Kalb s.n. (hb. Kalb, holotype).

Asterothyrium leucophalatum (Müll.Arg.) R.Sant.: **Costa Rica, Lücking 92-47 (hb. Lücking).**

Ecuador, Lücking 96-241 (hb. Lücking).

Brazil, Malme 414:2 (S), 414:3 (UPS, comm. Rick s.n. (S)).

Argentina, Henssen 24112b & Vobis (hb. Henssen).

Asterothyrium longisporum Lücking: Ecuador, Lücking 96-266 (hb. Lücking).

Asterothyrium octomurum R.Sant. (type species of Stictoptelopha nom. inval.): **Guinea, Lisowski 1157 (hb. Vezda).**

IVORY COAST, Santesson 10740 (UPS).

DR Congo, Vandepeer 38503 (UPS, holotype).

Asterothyrium pittleri Müll.Arg. (type species of Diplolophasia): **Costa Rica, Pittier & Tonduz 6025 (BM).**

Pittier 5110 (G, holotype), Lücking 91-52 (hb. Henssen, hb. Lücking).

Ecuador, Lücking 96-216 (hb. Lücking).

Ivory Coast, Santesson 10497 (UPS).


Lücking 92-48 (hb. Lücking, Ecuador, Lücking 96-240 (QCA). **Peru, Santesson & Thor (UPS).**

Brazil, Lücking s.n. (hb. Henssen, hb. Lücking, Theissen s.n. (S)); ibid., comm. Rick s.n. (S).

Paraguay, Balansa 4013 (G, holotype). **Argentina, Henssen 24112c & Vobis (hb. Henssen).**

Ivory Coast, Santesson 10434 (UPS).


Brazil, Baker s.n. (S).

Asterothyrium tetrasporum Lücking: **Costa Rica, Lücking 88-39 (ULM, holotype).**

Asterothyrium umbilicatum (Müll.Arg.) Müll.Arg. (type species of Actinotheichas): **Costa Rica, Lücking 91-23 (hb. Lücking).**

Ecuador, Lücking 96-338 (hb. Lücking).

Brazil, da Silva s.n. (URM 46652, holotype of Actinotheichas maranhensis Cavalc. & Porocah).

Paraguay, Balansa 4013 (G, holotype).

Asterothyrium uniseptatum Lücking: Honduras, Standley 7703 (UPS).

Costa Rica, Lücking 91-54 (hb. Lücking).

Paraguay, Schinini & Bordas 20792 (CTES).

Asterothyrium sp. (p. enchiadis). **Brazil, Malme 414:3 (S, filed as A. leucophalatum).**

Gyalidea astercus (Anzi) Aptoott & Lücking (type species of Solorinella): **U.S.A., Thor 8888 (S).**

Switzerland, Theobald s.n. (UPS). Czech Republic, Sica s.n. (UPS).

Gyalidea ephiphylla Veza: **Costa Rica, Lücking 91-1844, 91-5664 (both hb. Lücking).**

Guinea, Lisowski s.n. (hb. Vezda, holotype).


Gyalidea hylainecens (Nyl.) Veza: [incl. var. mexicana (B.delesd.) Veza].

Costa Rica, Sipman 12387 (B).

Ecuador, Cleveland 20555 (B; Veza: Lich. Sel. Exs. 3506).


Portugal, Henssen 2554s (hb. Henssen).

Gyalidea lecanorina (Knight) P.James & Galloway: **New Zealand, Henssen 30360a (hb. Henssen).**

Gyalidea le工业企业isopsis (A.Massal.) L. ex Veza. Var. Veza: **Costa Rica, Veza: 78 (hb. Veza, holotype).**

Gyalidea multispispora (Anz) Lambus & Veza: **Papua New Guinea.**

Aptoott 178199 (B).


Guinea, Lisowski s.n. (hb. Vezda, holotype). **Ivory Coast, Santesson 10741: 4 (UPS).**

Gyalidea praetermissa Foulac & Thor: **Sweden, Foulac & Thor s.n. (UPS, holotype).**

Psorotheciopsis albomaculans (Rehm) Veza: **Costa Rica, Lücking 92-4705 (hb. Lücking).**

Psorotheciopsis guajalitensis Lücking: **Ecuador, Lücking 96-181 (hb. Lücking).**

Psorotheciopsis gyalideoides (Veza) Henssen & Lücking: **Guinea, Lisowski 1118 (hb. Veza).**

Psorotheciopsis patellaroides (Rehm) R.Sant. (type species of Linhartia): **Costa Rica, Lücking 92-1811 (hb. Lücking).**


Psorotheciopsis premneella (Müll.Arg.) R.Sant. (type species of Psorotheciopsis): **Costa Rica, Lücking 88-593 (hb. Lücking).**

Brazil, Puiggari 2803 (G, holotype). **Ivory Coast, Santesson 10614 (UPS).**

Togo, Hughes 968 (UPS). **Psorotheciopsis var. var. secolare (Veza) Henssen & Lücking:**

Guinea, Lisowski 1175 (hb. Veza, holotype).
Specimens were studied under a Wild M7 dissecting microscope and a Zeiss dissecting microscope (8–50×). Thin sections of thallus, apothecia and pycnidia of different developmental stages were made with a freezing microtome. Sections were stained in Lacto-Glycerine/Cotton-Blue (LB) and studied under a Wild M20 compound microscope and a ZEISS microscope (32-1000×). Hand sections and squeeze mounts were further used to study paraphyses, asci and ascospores. I$_{lugu}$ (I) and KOH (K) were applied for microchemical tests (I+/−: Lugol only; KI+/−: Lugol after pretreatment with KOH). Anatomical photographs were made with a Wild M20 compound microscope, using Kodak professional film 5-TMX 120 in 6 × 6 cm format. Habit photographs were made with a Wild M7 dissecting microscope and a Nikon F301 camera with 4:1/90 mm macro combination, using Kodak professional film 5-TMX 120 in 6 × 6 cm format and Fuji Sensia II 100 colour slide in 36 × 24 mm format.

Terminology follows Henssen and Jahns (1973) and Henssen (1981). Hypothecium refers to the layer below the hymenium including ascogeneous hyphae (sometimes called subhymenium by other workers). True paraphyses grow vertically with free tips, while paraphysoids are branched and anastomosing and frequently develop first from the generative tissue and are later replaced by true paraphyses. Periphysoids develop as lateral paraphyses from the proper excipulum into the cavity between excipulum and hymenium. Plasma-rich generative tissue is identified by its strong stain in LB. In hemi-angiocarpous apothecia, the generative tissue develops a roof that encloses the hymenium and is separated from the latter by a split. The roof, together with adjacent thallus tissue, form the covering layer.

Results

Thallus morphology and anatomy

Gyalidea (including Solorinella) forms diffuse, hardly delimited thalli on soil and rock surfaces. Some species grow on bryophytes, dead plants and bark, while Gyalidea epiphylla and G. phyllophila are foliolicous (Figs. 1, 6A and 7A). In foliolicous species, the thallus is small and thin and partly dispersed into rounded patches, while in saxicologous and terricolous taxa it can cover large areas of the substrate and, if well-developed, be up to 500 µm thick and fissurate-areolate. Otherwise, the thallus is typically smooth to minutely farinose.

In cross sections of Gyalidea species, three layers are usually visible: a more or less indistinct, cartilaginous cortex (absent in species with thin thallus), a single- to multilayered algal layer with dense arrangement of chlorococcoid algal cells, and an indistinct to well-developed medulla composed of interwoven hyphae which, in saxicologous and terricolous taxa, encloses substrate particles.

The thallus in Psorotheciopsis and Asterothyrium consists of dispersed, eventually confluent patches 1–3 mm across, which are connected by an invisible prothallus formed by hyaline hyphae. Depending on the species, the patches exhibit a characteristic, greyish to silvery white colour (Figs. 2–3, 8A, 9A–B and 14A). In Psorotheciopsis patellarioides and Asterothyrium atromarginatum, the margin of the thallus patches is bordered by a thin, blackish line, caused by dark pigmented cortical cells at the periphery of the thallus (Figs. 2B and 8A). Most species have a thin, translucent prothallus free of algal cells.

A section through the thallus of Psorotheciopsis and Asterothyrium reveals up to four strata: (1) a cellular cortex, (2) an uni- to multistratose algal layer, (3) a more or less well-developed medulla, and (4) a thin submedullary layer (Fig. 4). The cortex is one of the most distinctive features in the two genera, consisting of dead, rectangular cells which, when seen from above, form a unistratose layer of branched, radiate cell rows, similar to the thallus of a free-living Phycopeltis alga (Fig. 5). This cortex is responsible for the whitish thallus colour, since the dead, rectangular cells are physically light-reflective.

Depending on the thickness of the thallus, the algal layer consists of 1–3 irregular strata of rounded, 4–8 µm large cells. The phycobiont seems to be Trebouxia in all studied cases. Below
the algal layer, a medullary tissue may be developed, which consists of rather loosely packed hyphae with inflated, 4–6 µm broad cells which do not stain in LB. It is particularly conspicuous in thick thalli of *Asterothyrium leucophthalmum*, *A. rotuliforme* (Fig. 4B), and *A. umbilicatum* (Fig. 14E), but inconspicuous or absent in other species, e.g. *Psorotheciopsis patellarioides* (Fig. 4A). Below the medullary tissue, a thin, irregular tissue of small (ca. 2 µm in diam.), plasma-rich cells is found (Fig. 4A–B).

**Apothecial morphology, anatomy and ontogeny in Gyalidea**

Apothecia are typically sessile and basally constricted (*Gyalidea hyalinescens*), but may remain semi-immersed or immersed-erumpent in *G. lecanorina*, *G. praetermissa*, *G. multispora*, and *G. astericus* (Figs. 1A–F, 6A–B and 7A). The lateral excipulum is hyaline or partly pigmented (e.g. in *G. lecideopsis* and *G. fritzei*), giving the apothecia a biatorine or lecideine appearance (Figs. 1A, 6A–B and 7G–H). The basal part is continuous (cupular excipulum; Fig. 7B and F), or sometimes thin and interrupted (annular excipulum; Fig. 6B and F). The apothecial margin can form small to rather large teeth and be covered with remnants of thallus tissue (Figs. 1B–F and 7B). In sections of mature apothecia, the lateral excipulum is conspicuously enlarged and in most species composed of branched and partly anastomosing hyphae embedded in a gelatinous matrix (Fig. 7B, E and G–H). In a few species, these hyphae are compacted to form a paraplectenchymatous tissue, as in *Gyalidea epiphylla*, *G. phylophila*, and *G. lecanorina* (Figs. 6G and 7F).

In *Gyalidea lecanorina*, the primordium differentiates into a globose structure with paraplectenchymatous roof and a nucleus with paraphysoids and basal ascogeneous hyphae being surrounded by a cupular excipulum.

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**Fig. 1. General habit of Gyalidea species. — A–B: Gyalidea hyalinescens (A: Costa Rica, Sipman 12387; B: Ecuador, Culberson 20555); note the small teeth on the apothecial margin in B. — C: G. phylophila (holotype); thallus with three apothecia. — D: G. multispora (Papua New Guinea, Aptroot 17819b); note the distinct marginal teeth of the apothecia. — E–F: G. astericus (E: Switzerland, Theobald s.n.; F: Czech Republic, Susa s.n.); note the well-developed, triangular marginal lobes. Scale for A–B = 2 mm, C = 0.7 mm, D–F = 1.2 mm.**
Along with the rupture of the paraphysoids and vertical growth of true paraphyses, the roof ruptures in upper part to expose the hymenium (Fig. 6D–F). The uppermost parts, which later form the edges of the excipulum, thereby retain short periphysoids (Fig. 6F). In the mature apothecium, the lateral parts of the excipulum are ± paraplectenchymatous in upper
Fig. 3. General habit of *Asterothyrium* species. — A: *A. argenteum* (Costa Rica, Lücking 91-131); the pale apothecial disc is partly covered by unpigmented teeth. — B: *A. gyalideoides* (an isotype); note the sessile apothecia and pycnidia with extruded conidial mass (arrow); no thallus margin is apparent around the apothecia. — C: *A. octomerum* (Guinea, Lisowski 1157); dispersed thallus with several apothecia. — D: *A. septemseptatum* (Costa Rica, Lücking 92-48a); the oldest apothecia in the centre surrounded by a whitish area, while the apothecial teeth are reduced and very thin. — E: *A. anomalum* var. *anomalum* (Argentina, Vanni et al. 3654); the apothecial discs partly covered by blackish marginal teeth. — F: *A. rotuliforme* (Brazil, Lücking s.n.); the oldest apothecia in the centre surrounded by a whitish area, and the apothecial teeth completely reduced. Note the external similarity between *A. octomerum* (ascospores 7-septate) and *A. anomalum* (ascospores muriform) on one hand and between *A. septemseptatum* (ascospores 7-septate) and *A. rotuliforme* (ascospores muriform) on the other. — G: *Asterothyrium microsporum* (Costa Rica, Lücking 91-3460); sterile specimens with marginal, squad-conoid pycnidia (type II). — H: *A. umbilicatum* (Costa Rica, Lücking 91-23), sterile specimens with centrally immersed, applanate pycnidia (type III). Scale = 1 mm, for B and H = 0.7 mm.
and outer parts but composed of parallel, radiating hyphae in inner parts close to the hymenium; its uppermost parts are pigmented, while its lateral parts are covered with algiferous thallus tissue where the apothecia are semi-immersed in the thallus (Fig. 6G).

Apothecial primordia in *Gyalidea hyalinescens* appear as globose structures composed of short cells strongly staining in LB (Fig. 7C). In later stages, the roof and lateral excipulum are comparatively thin and composed of densely packed, interwoven hyphae; asci develop rather soon (Fig. 7D). Mature apothecia feature a mostly hyaline excipulum composed of densely packed, parallel and radiating hyphae, pigmented in upper part and laterally covered by a thin, amorphous thallus tissue containing algal cells (Fig. 7E). In *G. lecideopsis* var. *lecideopsis*, the rupturing roof forms rather thick edges (Fig. 7G), as is also seen in *Psorotheciopsis* (see below).

*Gyalidea asteriscus* is characterized by its comparatively large, immersed-erumpent apothecia that feature distinct, more or less triangular lobes (Fig. 1E–F). In section, these lobes are composed of branched and partly anastomosing, parallel and more or less radiate hyphae with thin lumina and thick, strongly gelatinizing walls. In the lower, outermost parts, a more or less well-developed thallus tissue covers the excipulum. We were unable to study young stages of apothecia, but from the structure of the apothecia in *Gyalidea asteriscus*, the rupture of the roof forms thick edges (Fig. 7G), as is also seen in *Psorotheciopsis* (see below).
Fig. 6. Apothecial anatomy and ontogeny in *Gyalidea lecanorina* (New Zealand, Henssen 30360a; B–H microtome sections in LB). — A: General habit; note the semi-immersed apothecia surrounded by a whitish thallus rim. — B: Section through mature apothecium; note the well-developed, annular excipulum basally and laterally surrounded by algiferous thallus tissue. — C: Primordium with nucleus of strongly staining hyphae (paraphyses and subhy- menium) and paraplectenchymatous roof (arrow). — D: Young apothecium opening by an apical fissure in the roof; note the external thalline tissue on the roof. — E–F: Young apothecium with open roof; the lateral hyphae of the hamathecium are connected to the roof, and their upper parts resemble periphysoids (arrow); note the annular excipulum in F. — G: Margin of mature apothecium; note the apically paraplectenchymatous excipulum which is connected to parallel-radiate hyphae near the hymenium. — H: Section through pycnidium. Scale for A = 1 mm, for B, D–F = 50 µm, for C, G–H = 20 µm.
Fig. 7. Apothecial anatomy and ontogeny in Gyalidea (B–H microtome sections in LB). — A–E: Gyalidea hyalinescens. — A: General habit (Canada, Vezda: Lich. Sel. Exs. 1427); note the finely dentate apothecial margins. — B: Section through mature apothecium (Portugal, Henssen 25545a); note the external algiferous thallus tissue covering the lateral excipulum. — C: Primordium of strongly staining cells (Canada, Vezda: Lich. Sel. Exs. 1427). — D: Young apothecium with developing asci (Portugal, Henssen 25545a); note the closed roof and excipulum. — E: Margin of mature apothecium (Portugal, Henssen 25545a); border between hymenium and excipulum of mature apothecium showing periphysoids (arrow). — F: G. phyllophila (Georgia: Vezda s.n.; Vezda: Lich. Sel. Exs. 1569), section through mature apothecium with paraplectenchymatous excipulum (arrow). — G: G. lecideopsis (Slowakia, Vezda 26342); section through young apothecium showing large edges formed by the roof. — H: G. fritzei (Slowakia, Vezda s.n., Vezda: Lich. Sel. Exs. 533); section through mature apothecium showing apically pigmented excipulum (arrow). Scale for A = 1 mm, for B, D, G–H = 50 μm, for C, E–F = 20 μm.
ecial margin we assume that the young apothecia have a well-developed covering layer composed of roof and thallus tissue, which is turned upside-down after rupturing and exposure of the hymenium. Since the lateral lobes are much larger than the young primordia, we suspect that roof and lateral excipulum enlarge secondarily after rupturing, a phenomenon which is also found in *Asterothyrium rondoniense* (see below).

**Apothecial morphology, anatomy and ontogeny in *Psorotheciopsis***

Apothecia in *Psorotheciopsis* are sessile and not covered by thallus tissue laterally (Figs. 2A–D and 8A). Most species have lecideine, pure black apothecia, such as *P. albomaculans* or *P. premneella* (Fig. 2C–D), or a black margin combined with a pale disc, like *P. patellarioides* (Figs. 2B and 8A), while *P. gyalideoides* features translucent apothecia (Fig. 2A). The apothecial margin is usually smooth and not prominent, but might produce small, teeth-like protuberances in *P. patellarioides* and *P. variiseptata*. The lateral excipulum is composed of slightly branched hyphae embedded in a gelatinous matrix. External parts of the excipulum are hyaline, while internal and basal parts are mostly black pigmented (Fig. 8B–I).

Apothecia are either formed on the algiferous thallus patches, as in *Psorotheciopsis guajalitenesis*, or marginally on the hyaline prothallus, as in *P. patellarioides* and *P. albomaculans* (Figs. 2B–C and 8A). In *P. patellarioides*, the primordium is seen as applanate generative tissue which differentiates a heavily pigmented roof (Fig. 8C). The primordium is covered by thallus tissue, which in early stages is difficult to tell apart from the generative tissue but soon ruptures and separates from the proper roof. Soon after, a cavity between hymenium and roof is formed, and the proper roof ruptures in the centre (Fig. 8C–D). In that stage, the roof typically appears as ± black, triangular structure in section, which its thickest parts oriented towards the centre and its tapering sides lateral of the hymenium.

With the growth of the hymenium and maturation of asci, the roof is further torn aside by prolongation of the paraphyses and finally integrated into the apothecial margin, where it forms the innermost, pigmented part of the proper excipulum (Fig. 8B). In mature apothecia, the roof is not or only slightly elevated above the hymenium surface and sometimes forms short, irregular teeth. A particular feature is the secondary growth of slightly branched hyphae from the lateral and basal part of the roof (Fig. 8E–G); these hyphae are embedded in a gelatinous matrix and, in mature apothecia, form the major part of the proper excipulum (Fig. 8B). Since these hyphae originate from the roof, i.e. the generative tissue, they are part of a true excipulum and are not to be confused with a zeorine thallus margin. Due to the growth of these secondary excipular hyphae, the thallus tissue which originally covered the primordium is bent down towards the leaf surface and finally hidden below the mature apothecium, where it is visible as a strongly recurved black line (Fig. 8B).

Apothecial development in *Psorotheciopsis premneella* resembles that of *P. patellarioides*. Young stages exhibit a black roof which, in sections, ruptures into ± triangular halfs (Fig. 8H). Again, the thin thallus tissue originally covering the primordium is pushed away by the growth of secondary hyphae from the lateral and basal part of the roof, and the excipulum of mature apothecia is composed of slightly branched hyphae embedded in a gelatinous matrix, very much like in *Gyalidea*, while the original roof is ± reduced (Fig. 8I). As in *P. patellarioides*, the thallus tissue originally covering the primordium remains as a straight to strongly recurved black line near the apothecial base, while the basal part of the excipulum remains small and hyaline.

**Apothecial morphology, anatomy and ontogeny in *Asterothyrium***

The apothecia of *Asterothyrium* are typically immersed in the thallus but erumpent and eventually prominent when mature. Mature apothecia feature a thallus margin composed of obliquely oriented, triangular lobes or teeth covering the apothecial disc (Figs. 2E–H, 3A, C, E and 9A–B). In *A. chroodisciforme* and *A. rondoniense*, the thallus teeth are recurved and give the apothecia a characteristic, star-like appearance.
Fig. 8. Apothelial anatomy and ontogeny in *Psorotheciopsis* (B–I microtome sections in LB). — A–G: *P. patellarioides* (Guinea, *Lisowski s.n.*; Vezda: Lich. Sel. Exs. 1158). — A: General habit; note the thin black lines around the thallus patches and the formation of the apothecia between the thallus patches on an algal-free prothallus. — B: Mature apothecium; the roof is visible as black inner part of the excipulum, while the black thallus tissue remains as a strongly bent line at the lateral apothecial base (arrow). — C: Young apothecium, with the roof centrally ruptured; note the cavity between the upper part of the hymenium and the roof; the thallus tissue begins to separate laterally from the roof (arrows). — D: Subsequent stage, with paraphyses and black roof; the thallus tissue has ruptured and covers the lateral parts of the roof (arrows). — E–G: Development of excipulum; the black inner part of the proper excipulum represents the original roof from which, secondarily, branched hyphae embedded in a gelatinous matrix are growing out; the black thallus tissue which originally covers the primordium is bent down towards the leaf surface by the growth of the proper excipulum while the original roof remains in the upper part of the excipulum (arrows). — H–I: *P. premneella* (holotype). — H: Young apothecium with immature asci and thick black apical roof that ruptured in the centre. — I: Marginal part of mature apothecium with asci and ascospores; the original black roof has almost completely disappeared and is replaced by the secondary excipulum composed of short hyphae embedded in a gelatinous matrix. Scale for A = 1 mm, for B–C and E–I = 20 µm, for D = 50 µm.
In *A. rotuliforme*, and partly also in *A. leptosporum*, the thallus margin is entire, with no teeth visible (Fig. 3F). Reduced, very small or short teeth are found in *A. anomalum* var. *pallidum* and *A. septemseptatum* (Fig. 3D–E). In *A. gyalideoides*, the mature apothecia are sessile, and the excipulum is not covered by adjacent thallus tissue (Fig. 3B). Interspecific variation is mainly found in apothecial size and the colour of disc and margin.

In *Asterothyrium anomalum* var. *pallidum*, *A. argenteum*, *A. monosporum*, and *A. uniseptatum*,
the marginal teeth are pale (Figs. 2H and 3A), while *A. anomalum* var. anomalum, *A. aulaxi- noides, A. leucophthalum, A. octomerum, A. pittieri* and *A. tetrasporum* have grey to brownish black teeth (Figs. 2E–F, 3C, E and 9A–B). The disc might be pale and translucent in *A. argenteum, A. aulaxinoides*, and *A. microsporum* (Figs. 2E and 3A), yellowish to reddish brown in *A. monosporum, A. rondoniense*, and *A. unisep- tatum*, or brownish black in *A. chroodisciforme, A. pittieri* and *A. tetrasporum* (Fig. 2F–G). In most species, the small thallus patches produce a single, central apothecium (Figs. 2H and 3A), but eventually become confluent to form a polycarpous thallus (Figs. 2F, 3C and 9A). In *A. septemseptatum* and *A. rotuliforme*, the single thallus patches are polycarpous from the beginning, with 1–2 central apothecia surrounded by a concentric ring of 5–15 apothecia. The central apothecia are usually older and larger and surrounded by a whitish area (Fig. 3D and F).

The apothecia of *Asterothyrium* have a very characteristic anatomy. The proper excipulum is paraplectenchymatous and distinctly cupular, visible as a thin layer below the hypothecium (Figs. 9F and 10D), and reacts I+ red. *Asterothyrium chroodisciforme* and *A. rondoniense* differ from the general pattern in having the excipulum composed of branched, net-like hyphae embedded in a gelatinous matrix, with a large extension of the lateral part (Fig. 11A–D). In all species, the basal part of the apothecium is formed by a thin layer of small, shortly anticlinal cells (Fig. 10D). The excipulum is laterally covered by thallus tissue which may contain dark pigments in the cell walls and is covered by the cellular thallus cortex (Figs. 9F, 10C and F–G). In *A. gyalideoides*, the paraplectenchymatous excipulum is laterally free and not covered by thallus tissue (Fig. 10L). *Asterothyrium rotuliforme* is the only species which retains epithelial algae (Fig. 12).

The typical apothecial ontogeny is found in *Asterothyrium leucophthalum, A. argenteum* (the type species), *A. pittieri*, and *A. monosporum*. In *A. leucophthalum*, the disc of mature apothecia is covered by teeth-like remnants of the covering layer in the dry condition but exposed in the wet condition (Fig. 9A–B). The lens-shaped to globose generative tissue is formed at the thallus base by irregularly arranged, short-celled hyphae strongly staining in LB (Fig. 9C). In young apothecia, mainly true paraphyses are formed by vertical growth of hyphae within the generative tissue. The basal part of the primordium develops into a thin hypothecium, while its periphery differentiates into a paraplectenchymatous cortical layer, which later forms the basal and lateral excipulum, and the paraplectenchymatous roof being separated from the hymenium by a narrow cavity (Fig. 9D–E). The roof is covered by a dark pigmented thallus tissue, the pigments being deposited in the walls of the vegetative thallus hyphae below the cortex, which itself remains unpigmented. The lateral parts of the excipulum are rather thin and not well separated from the thick, dark hypothecium and the lateral parts of the hymenium. In the mature apothecium, the hymenium is still surrounded by a cup-shaped excipulum and a pigmented thallus tissue, both being closely adnate and surpassing into the overarching teeth (Fig. 9F).

Developmental morphology in *Asterothyrium argenteum* corresponds closely to that found in *A. leucophthalum*. The covering layer above the cavity of young apothecia is composed of the paraplectenchymatous roof and a thick layer of dark pigmented thallus tissue including the hyaline cortex (Fig. 10A–B). In mature apothecia, the thallus tissue might apically separate from the paraplectenchymatous excipulum which itself arises from periclinally arranged hyphae (Fig. 10C). In *A. pittieri*, ascus initials might be visible in the primordium (Fig. 10E). In most species, a split is formed between the hymenium and the lateral excipulum (Figs. 9F, 10F–G and 10I).

A particular feature of most *Asterothyrium* species is the intimate connection between the paraplectenchymatous roof and the adjacent thallus tissue to form a multistratose covering layer, composed of the thallus cortex, the often pigmented subcortical thallus tissue lacking algal cells, and the paraplectenchymatous roof. In young apothecia, e.g. of *A. leucophthalum* and *A. argenteum*, this covering layer ruptures in the centre (Figs. 9D–E and 10A–B). Along with the growth of the hymenium and maturation of asci and ascospores, the ruptured covering layer is pushed away laterally, but remains lateral of the hymenium in mature apothecia, its remnants being visible as triangular teeth partly covering...
Fig. 10. Apothecial anatomy and ontogeny in *Asterothyrium* (microtome sections in LB). — **A–D**: *A. argenteum* (Costa Rica, Lücking 91-44). — **A**: Young apothecium, same stage as in Fig. 9D, the covering layer rupturing in the centre. — **B**: Subsequent stage, the covering layer largely ruptured; note the connection between the paraplectenchymatous lateral part of the proper excipulum and roof and the basal part of the excipulum, composed of parallel hyphae. — **C**: Marginal part of mature apothecium; the corticate thallus tissue partly separated from the lateral excipulum (arrow). — **D**: Central part of mature apothecium; note the paraplectenchymatous excipulum basally composed of small, shortly anticlinal cells (arrow). — **E–G**: *A. pittieri* (E: Costa Rica, Lücking 91-52; G: Costa Rica, Pittier & Tonduz 6025). — **E**: Primordium with ascus initials, covered by a pigmented, corticate thallus tissue; the roof is not yet apparent. — **F–G**: Marginal parts of mature apothecia, same stage as in Fig. 9F and 10C; the lateral tooth composed of the internal paraplectenchymatous roof or proper excipulum (ro) and the closely adnate, pigmented and corticate thallus tissue (th). — **H**: Central part of mature apothecium with hymenium, showing mature ascus with ascospores. — **I–K**: *A. anomalum var. pallidum* (Costa Rica, Lücking 92-51). — **I**: Marginal part of mature apothecium of a specimen with reduced teeth; note that the thallus tissue covering the paraplectenchymatous proper excipulum carries algal cells in its lower part; excipulum and thallus tissue are largely confluent and not well separated. — **K**: Young ascus; the immature ascospore which later becomes muriform closely resembles the mature ascospores in *A. octomerum*. — **L**: *A. gyalideoides* (an isotype); marginal part of mature apothecium, the lateral excipulum not covered by thallus tissue; note the short periphysoids (arrow). Scale for **A, F, H** = 50 µm, for **B–D, G, I–K** = 20 µm, for **E** = 10 µm.
the apothecial disc (Fig. 2F and H). In that way, the lateral parts of the original roof are integrated into the cup-shaped excipulum of mature apothecia, while the central parts remain in the overarching teeth. The internal structure of the teeth is the same as in the original covering layer, with the thallus cortex, the pigmented subcortical thallus tissue, and the paraplectenchymatous excipulum or roof (Figs. 9A, F and 10F–G).

A slightly deviating pattern is found in Asterothyrium gyalideoides. The apothecial ontogeny chiefly follows that of A. argenteum, but the covering thallus tissue is unpigmented from the beginning and already in young apothecia separates from the paraplectenchymatous roof. The roof itself ruptures earlier than in other species and is soon pushed away laterally. In mature apothecia, the margin is thus only formed by the proper excipulum that is not covered by thallus tissue (Figs. 9A, F and 10F–G).

Fig. 11. Apothecial anatomy and ontogeny in Asterothyrium rondoniense (microtome sections in LB; A, D: Costa Rica, Pittier & Tonduz 6025; B–C: Brazil, Baker s.n.). — A: Young apothecium, roof composed of branched, net-like hyphae partly connected to the upper part of the paraphyses as paraphysoids (arrow). — B: Subsequent stage, the covering layer partly rupturing. — C: Mature apothecium, the internal part (roof and excipulum) of the lateral tooth composed of branched hyphae embedded in a gelatinous matrix (arrow). — D: Same stage but other side of apothecium, again with excipulum composed of branched hyphae in a gelatinous matrix (arrow); note that the proper excipulum is not well separated from the covering, unpigmented thallus tissue (arrow). Scale for A = 20 μm, for B–D = 50 μm.

A strongly deviating pattern is found in Asterothyrium gyalideoides. The apothecial ontogeny chiefly follows that of A. argenteum, but the covering thallus tissue is unpigmented from the beginning and already in young apothecia separates from the paraplectenchymatous roof. The roof itself ruptures earlier than in other species and is soon pushed away laterally. In mature apothecia, the margin is thus only formed by the proper excipulum that is not covered by thallus tissue (Fig. 10L), and projecting teeth are not apparent (Fig. 3B).

Apothecial anatomy and ontogeny in Asterothyrium rondoniense exhibit a third pattern of apothecial development, which differs in that the roof and excipulum are not paraplectenchymatous but composed of branched, net-like hyphae embedded in a gelatinous matrix, very much like the excipular structure in Gyalidea (Fig. 11A–B). In the lateral parts of the apothecia, the paraphysoids are more distinctly seen than in other species (compare Figs. 10B and 11A), while the remaining interascal hyphae are true paraphyses. A strand of densely interwoven hyphae arises in the upper part of the gelatinous roof underneath the unpigmented thallus tissue, and the roof breaks up by several splits (Fig. 11B). In mature apothecia, the thick lateral teeth are recurved
and expose the inner surface of the original roof, retaining their gelatinous structure with radiating hyphae and being separated from the hymenium by a split (Fig. 11C–D).

*Asterothyrium rotuliforme* differs from all other species of the genus by the presence of epithecial algae. The primordium arises at the base of the often thick thallus and is covered by a corticate thallus tissue in which the pigmentation is much reduced and which includes algal cells (Fig. 12A). The generative tissue is composed of densely aggregate, short-celled hyphae and in upper part encloses cells of the phycobiont. The roof of the primordium is rather thin and more or less directly formed beneath the thallus cortex; it incorporates the algal cells above the generative tissue which immediately begin cell division (Fig. 12B–C). The algal cells multiply in the cavity, the roof, the marginal parts of the young apothecium, and partly between the paraphyses. With the formation of the roof, the cavity which separates roof and hymenium becomes visible (Fig. 12B and D). Contrary to other species of *Asterothyrium*, the covering layer, mainly formed by

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**Fig. 12. Apothecial anatomy and ontogeny in *Asterothyrium rotuliforme* (microtome sections in LB; A–D: Costa Rica, Lücking 92-2; E–F: Brazil, Rick s.n.).** — A: Generative tissue covered by unpigmented, corticate thallus tissue; note the algal cells enclosed in the upper part. — B: Primordium with ascus initials; note the cavity (arrow) between the upper part of the hymenium and the roof, which itself is not well developed and laterally connected to the excipulum. — C: Lateral section of young apothecium with covering, corticate thallus tissue; note the algal cells above the hymenium in state of division. — D: Central section of same young apothecium with two ascus initials; note again the distinct cavity (arrow) between the upper part of the hymenium and the roof containing the algal cells. — E: Mature apothecium with ascospores and abundant epithecial algae. — F: Marginal part of apothecium; note the connection between the paraplectenchymatous lateral part of the proper excipulum and the basal part of the excipulum, composed of parallel hyphae (arrow). Scale for A–D, F = 20 µm, for E = 50 µm.
the thin roof and the thallus cortex and including the algal cells, does not rupture, but disintegrates completely to liberate the algal cells which then become epithelial algae (Fig. 12E–F). Therefore, in mature apothecia the lateral margin is formed by the proper excipulum and a thallus tissue that basally includes algal cells, while teeth are not apparent. The structure of the excipulum is the same as in other species, however, and like in A. argenteum, the transition between the basal vertical hyphae and the lateral paraplectenchymatous excipulum is visible (Fig. 12F).

**Hymenium, ascus structure and ascospores**

The hamathecium in Gyalidea, Psorotheciopsis and Asterothyrium consists of true, unbranched paraphyses which are not distinctly thickened at their apices (Figs. 7B, E–F, 8B, G, I, 9E–F, 10C, G–I, 11D and 12E). The paraphyses are only weakly gelatinized and easily separable in squash mounts. The asci are more or less clavate, and immature asci exhibit a more or less distinct apical tholus. All parts of the ascus wall are I– and KI–, while the ascus lumen usually becomes I+ yellowish red to reddish brown (mostly the colour of the I-solution itself). In immature asci, a ring-like structure can be observed that projects downwards from the lower part of the tholus into the lumen. In broken asci, the tholus is seen as a more or less globose structure, and the ring-like structure as a reversed V-shaped ocular chamber extending basally into the ascus lumen. This ascus type is here called *Gyalidea* type, since it was first described for the genus *Gyalidea* (Vezda 1966). It is the same type as described by Hafellner (1984) for *Psorotheciopsis* premneella and *Asterothyrium argenteum*.

Ascospores in *Gyalidea* are typically thin-walled and slightly constricted at the septa. Septation ranges from transversely septate to submuriform (Fig. 13), and the number of ascospores per ascus varies mostly from eight to one. *Gyalidea asteriscus* and *G. multispora* have polysporous asci (30–60 ascospores per ascus), and 10–14 ascospores per ascus are found in *G. polyspora*. Most species of *Psorotheciopsis* have thin-walled, 1-septate ascospores, such as *P. patellarioides* (Fig. 8G), *P. gyalideoides*, *P. guajalitensis*, and *P. philippinensis*. Three further types are found (Fig. 13). In *P. variesepultum*, ascospores are thin-walled and irregularly 1–11-septate, with no constrictions visible. *P. albomaculans* has rather characteristic ascospores: the central septum is very thick (up to 2.5 µm) and provided with a very thin channel which connects both cells. In *P. premneella*, the ascospores are 1-septate as in most other species but very large and thick-walled and occur single in the asc (Fig. 8I). In certain stages, a narrow channel can be observed in the thick septum connecting both cells.

Ascospores in *Asterothyrium* are principally thin-walled and 1-septate, as in *A. microsorum*, *A. decipiens*, *A. argenteum*, and *A. gyalideoides* (Fig. 10C–D). Three distinct lines of ascospore variation are present (Fig. 13). In *A. leucophthalmum*, *A. leptosporum*, and *A. longisporum*, the ascospores become elongate to acicular and often break into halves. The ascospores of *A. decipiens* and *A. longisporum* are rather large and often have gelatinous outer walls, representing a transition towards the second type, i.e. the large, thick-walled ascospores found in *A. hedbergi*, *A. tetrasporum*, *A. pittieri* (Fig. 10H), *A. monosporum*, *A. uniseptatum*, *A. aulaxinoides*, *A. chroodisciforme*, and *A. rondoniense* (Fig. 11D). In these species, the number of ascospores is continuously reduced, from six to finally one per ascus. In *A. rondoniense*, the large, 2-septate ascospores might appear secondarily divided to resemble muriform ascospores.

A third type is found in *Asterothyrium semtexseptatum*, *A. octomerum*, *A. anomalum*, and *A. rotuliforme*, with multi-septate and muriform ascospores, respectively (Fig. 13). In these species, ascospores are basically thin-walled but exhibit a gelatinous outer wall in *A. octomerum*. The number of ascospores per ascus is variable but constant within a species: eight in *A. septemseptatum*, four in *A. octomerum*, and one in *A. anomalum* and *A. rotuliforme* (Fig. 12E). The young ascospores in *A. anomalum* and *A. rotuliforme* go through a 7-septate stage (Fig. 10K), very much resembling the mature ascospores of *A. octomerum* and thus demonstrating the close relationship between the transversely septate and muriform type.

**Pycnidia and conidia**

Pycnidia are rare in Gyalidea, but abundant and often found on otherwise sterile thalli of Psorotheciopsis and Asterothyrium. Since species often grow intermingled and the dispersed thallus patches are difficult to tell apart, one must be cautious when assigning pycnidia to a particular species. Being aware of that problem, we have only accepted pycnidia as belonging to a given species when they were found on thalli carrying both apothecia and pycnidia.

While pycnidia are rather uniform in Gyalidea, usually being immersed and flask-shaped (Fig. 6H), Psorotheciopsis and Asterothyrium exhibit three different pycnidial types. Type I
consists of immersed, flask-shaped pycnidia scattered over the thallus surface, similar to those of *Gyalidea*, often appearing as narrow, tubular openings surrounded by a thin darker thallus zone. Such pycnidia were found in *Asterothyrium argenteum*, *A. pittieri*, *A. septenseptatum*, *A. rotuliforme* (Fig. 14D), and *Psorotheciopsis philippinensis*. The conidia produced in these pycnidia are mostly small (5–7 × 1–1.5 µm), but acicular (25–30 × 1–1.5 µm) and 1-septate, as in *Asterothyrium rotuliforme* and *Psorotheciopsis philippinensis* (Fig. 15A and K), but acicular (25–30 × 1–1.5 µm) and 1-septate in *A. argenteum* (Fig. 15B).

Type II is rather abundant but mostly found on sterile thalli. The pycnidia are larger than in type I, squad-conoid in outline and formed superficially at incisions of the thallus margin (Figs. 3G and 14A–C). Their wall is heavily pigmented and appears black or greyish when seen from above. Pure black pycnidia producing small (6–7 × 2 µm), ellipsoid, unseptate conidia are typical of *Asterothyrium microsporum* (Fig. 15C), *A. decipiens*, and *A. hedbergii*. In *A. leucopthalum* (Fig. 14B) and *A. gyalideoides*, the pycnidia are covered by a thin thallus tissue and therefore greyish, and the conidia are narrower (5–7 × 1–1.5 µm) and fusiform (Fig. 15D). A pycnidial type resembling that of *A. leucopthalum* was found on a specimen from Brazil (Fig. 14C), but the conidia are much longer (up to 20 µm) and almost acicular (Fig. 15E). In most species, the conidia are often extruded through the pycnidial opening and appear as a translucent, yellowish brown mass resembling a beak. A true beak formed by the same tissue as the pycnidial wall is found in pycnidia of *Psorotheciopsis*, e.g. *P. patellarioides*, but these pycnidia are otherwise very similar to those of *Asterothyrium*.

The third pycnidial type (type III), consists of applanate, disc-like pycnidia immersed in the centre of the thallus patches or arranged in a concentrical manner (Figs. 3H and 14E–F). This type is known from several sterile species of *Asterothyrium*, namely *A. umbilicatum*, *A. aspidospermatis*, and *A. pernambucense*, whose relationships to fertile taxa cannot be established at present. Their generic identity is proved, however, by the thallus structure, which closely resembles that of *A. rotuliforme*, particularly through the well developed medulla (Fig. 14E). In specimens of *A. umbilicatum*, rudimentary apothecial primordia were found which resemble those of other *Asterothyrium* species. The pycnidia remain closed for a long time but finally open by narrow slits. The internal anatomy is similar to that of the other two types and resembles that of young apothecia, with a ± paraplectenchymatous proper wall covered by a corticate, pigmented thallus tissue. The conidia found in these pycnidia belong to four types: (1) small (3–4 × 1 µm), fusiform and unseptate in *A. pernambucense* (Fig. 15F), (2) intermediate (8–12 × 1–1.5 µm), narrowly fusiform and unseptate in *A. aspidospermatis* (Fig. 15G), (3) long (15–25 × 1–1.5 µm), acicular and unseptate or rarely 1-septate in *A. umbilicatum* (Fig. 15H), and (4) very long (35–50 × 1–1.5 µm), acicular to filiform and 1–3-septate in an undescribed species (Santesson 1952: p. 318; Fig. 15I). The pycnidia of type III were discussed by Santesson (1952) and described as a separate anamorph genus *Actinoteichus* (Cavalcante et al. 1971, Lücking et al. 1998).

**Discussion**

**Apothecial ontogeny and intergeneric relationships**

Apothecial ontogeny in the Asterothyriaceae is hemiangiocarpous (see also Henssen 1976, 1981). The generative tissue differentiates into an upper roof and lateral excipulum, and a lower part which develops into hymenium, hypothecium and basal excipulum. During the ontogeny, the roof ruptures and is pushed away in lateral direction by the growing hymenium. In mature apothecia, parts of the original roof remain as parts of the proper excipulum. The roof may be covered by a more or less distinct thallus tissue, to form a covering layer which, in immature apothecia, might be separated from the hymenium by a cavity. In species where the hymenium is exposed only late during the ontogeny, e.g. *Asterothyrium*, both the covering layer and the cave are well-developed, while in *Gyalidea* and *Psorotheciopsis*, they are much less distinct.
Although the three studied genera are more or less well distinguished, which was also confirmed by recent phylogenetic studies (Aptroot & Lücking 2002), transitional forms concerning the morphology, anatomy, and ontogeny, do occur. Psorotheciopsis differs from Gyalidea in its corticate thallus and black apothecia, but Psorotheciopsis gyalideoides has hyaline apothecia...
ecia with the same structure as most Gyalidea species, and G. lecideopsis features marginally black apothecia. The black roof in Psorotheciopsis might therefore be homologous to the hyaline roof found in Gyalidea. Ascospores in Gyalidea and Psorotheciopsis are basically of the same type, but while polyspored asci are not found in Psorotheciopsis, the latter features large, thick-walled ascospores in P. premneella similar to those present in several Asterothyrium species. In the latter, a continuous transitional series exists between different extremes, while in Psorotheciopsis, the ascospores types are more distinct between the species. Still, the large ascospores of P. premneella are connected to the small, thin-walled type via P. albomaculans, whose small ascospores having a very thick septum. Generic separation on account of the ascospore type into Psorotheciopsis s.str. and Linhartia is thus not justified, as already stated by Lücking (1999).

Psorotheciopsis and Asterothyrium share the corticate thallus but differ in the sessile vs. immersed-erumpent apothecia with overarching marginal teeth, and in the hyphal vs. paraplectenchymatous excipulum. Again, transitional species do occur: Asterothyrium gyalideoides has sessile apothecia without marginal teeth, resembling Psorotheciopsis gyalideoides but differing in its paraplectenchymatous excipulum, while Asterothyrium chroodisciforme and A. rondoniense feature a hyphal excipulum similar to that found in Gyalidea. They also correspond to Gyalidea astericus in exhibiting secondary growth of the marginal teeth. A paraplectenchymatous excipulum is found in some Gyalidea species as well. Ascospore variation in Asterothyrium is greater than in the other genera but basically the same (Lücking 1999): the thick-walled ascospores of Asterothyrium pittieri and related species correspond to those of Psorotheciopsis premneella, while multiseptate and muriform ascospores are also found in Gyalidea.

All genera share a simple pycnidial type (I), while Psorotheciopsis and Asterothyrium feature a second, derived type (II), and Asterothyrium a third, very particular type (III). Thus far, no significant correlation has been found between the

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**Fig. 15.** Variation of conidial shape and septation in *Asterothyrium* and *Psorotheciopsis* (type of pycnidia indicated).

- A: *Asterothyrium rotuliforme*, fusiform conidia in pycnidia of type I.
- B: *A. argenteum*, acicular conidia in pycnidia of type I.
- C: *A. microsporum*, ellipsoid conidia in pycnidia of type I.
- D: *A. leucophthalmum*, fusiform conidia in pycnidia of type II.
- E: *Asterothyrium* sp., acicular conidia in pycnidia of type II.
- F: *A. pernambucense*, fusiform conidia in pycnidia of type III.
- G: *A. aspidospermatis*, bacillar conidia in pycnidia of type III.
- H: *A. umbilicatum*, acicular conidia in pycnidia of type III.
- I: *Asterothyrium* sp., filiform conidia in pycnidia of type III.
- K: *Psorotheciopsis philippinensis*, fusiform conidia in pycnidia of type I. Scale = 10 µm.
type of apothecia, pycnidia, and conidia produced by different species of *Asterothyrium*, but more material with conidiomata is required to study the possible taxonomic importance of pycnidial and conidial variation in this genus.

Perhaps the most particular species in *Asterothyrium* is *A. rotuliforme*, only recently included in the genus (Sérusiaux & de Sloover 1986). It is characterized by polycarpous thalli, a thick medulla, unpigmented apothecia without marginal teeth, disintegration of the roof during apothecial ontogeny, epithecial algae, and single, muriform ascospores. None of these characters are unique to this species, however, and hence separation to this species, however, and hence separation into a monotypic genus would not be justified. *A. septemseptatum*, too, has polycarpous thalli, while a thick medulla is found in *A. leucophthalmum* and *A. umbilicatum*. The disintegration of the roof during apothecial development and the lack of apothecial pigments and marginal teeth is correlated with the presence of epithecial algae, since these features are preconditions necessary to integrate the algal cells from the covering thallus tissue into the hymenium. The occurrence of epithecial algae itself is widespread among non-related lichens and often correlates with single, muriform ascospores, as for example in *Gyalideopsis vulgaris* (Müll.Arg.) Lücking, *Calenia monospora* Vezda, *Calenia aspidota* (Vain.) Vezda, and *Gyalectidium filicinum* Müll.Arg. in the Gomphillaceae, and *Sporopodium* in the Ectolechiaceae (Santesson 1952, Lücking 1997a).

Several features characteristic of *Psorotheciopsis* and *Asterothyrum* correspond to the particular ecology of these species, which are typically found on leaves in exposed microsites, such as the outer canopy of tropical rain forests (Lücking 1995, 1997b, 1999). The whitish thalli with a dead, cellular cortex that reflects light might be an adaptation to high light intensities. The same is true for the black pigmentation of the apothecium in *Psorotheciopsis* and the overarching teeth in *Asterothyrum*, possibly protecting the developing asci from excessive UV-radiation. The high variation of ascospore types in both genera is striking and might be explained by accelerated evolution caused by UV exposition, while the thick-walled ascospores could represent protection after dispersal. Hymenia in species of *Asterothyrum* and *Psorotheciopsis* are indeed frequently damaged (Santesson 1952, Lücking, pers. obs.).

The results presented here correspond well to the systematic redisposition of Asterothyriaceae by Lücking (1999) and Aptroot and Lücking (2002), who merged Linhartia with *Psorotheciopsis* and *Solorinella* with *Gyalidea*, and reinstated Asterothyriaceae sensu Eriksson and Hawksworth (1987) including the genera *Gyalidea*, *Psorotheciopsis*, and *Asterothyrium*. In this circumscription, the family is characterized by the following features: (1) hemiangiocarpous apothecial ontogeny, (2) true paraphyses, (3) I-negative hymenium, (4) "annelascaceous" asci (sensu Chadefaud 1973) of the *Gyalidea* type, and (5) chlorococcoid phycobiont.

**Systematic relationships of Asterothyriaceae**

The combination of features outlined above, especially apothecial ontogeny and ascus type, clearly place Asterothyriaceae within the Ostropales, together with the chiefly non-lichenized Stictidaceae and Odontotremataceae and the lichenized Gomphillaceae, Thelotremataceae, and Graphidaceae (Gilenstam 1969, Sherwood 1977, Scherwood-Pike 1987, Lücking 1997a, Lumbsch et al. 1997). Indeed, parallelisms to the developmental morphology in Asterothyriaceae are met with in other families of the order (Henssen & Jahns 1973, Henssen 1976, Sherwood 1977, Lücking 1997a). The formation of a roof and cavity in *Asterothyrium* corresponds to *Gyalectidium* (Gomphillaceae) and *Chroodiscus* (Müll. Arg.) Müll. Arg. (Thelotremataceae), while a gelatinous roof with netlike structure is found in *Graphina mendax* (Nyl.) Müll. Arg. (Graphidaceae). Similar trends are seen in *Absconditella* Vezda, *Cryptodiscus* Corda, and *Schizoxylon* Pers. (Stictidaceae). The lateral paraphysoids in *Gyalidea* and *Asterothyrium* are comparable to the paraphysoids in Gomphillaceae, while paraphyses similar to those of *Asterothyrium* are known from Thelotremataceae. Also in some species of *Schizoxylon*, the paraphyses are apically branched and resemble paraphysoids. Internal carbonisation of the proper margin is found in *Gyalideopsis* (Gomphillaceae), *Conotrema* Tuck. (Stictidaceae), and *Gyrostomum* Fr. (Graph-
idaceae). Schizoxylon shows a tendency towards polyspory, as in Gyalidea, but the mechanism is different (partition in the former, multiplication in the latter). Large, thick-walled ascospores are otherwise rare in the Ostropales but found, for example, in the non-lichenized Propolidium Sacc. (Stictidaceae). In Stictis and Biostictis Petr. (Stictidaceae), the host tissue covering the apothecia splits up into triangular lobes, very much like the overarching teeth in Gyalidea asteriscus and Asterothyrium, and species of Calenia and Aulaxina in the Gomphillaceae.

According to phylogenetic analyses (Dennetière & Péroni 1998, Lücking 1999, Aptroot & Lücking 2002), the following character states appear to be plesiomorphic/apomorphic in the Asterothyriaceae: (1) sessile/immersed-erumpent apothecia, (2) ecorcicorticrate thallus, (3) hyphal/paraplectenchymatous excipulum, (4) 8-spored/less than 8-spored or polyspored asci, (5) transversely septate/muriform ascospores, (6) thin-walled/thick-walled ascospores, (7) flask-shaped/squad-conoid/applanate pycnidia, and (8) non-folicicolous/folicicolous growth habit. The distribution of plesiomorphic features clearly identifies certain Gyalidea species as the basal group within the family. From there, different evolutionary trends are observed: (1) immersed-erumpent apothecia being laterally covered by overarching teeth (homoplastic in Gyalidea and Asterothyrium), (2) cellular thallus cortex (synapomorphic in Psorotheciopsis and Asterothyrium), (3) paraplectenchymatous excipulum (homoplastic in Gyalidea and Asterothyrium), (4) polysporous asci (possibly synapomorphic in Gyalidea), (5) large, thick-walled ascospores (homoplastic in Psorotheciopsis and Asterothyrium), and (6) specialized pycnidia (synapomorphic in Psorotheciopsis and Asterothyrium).

Since Gyalidea conforms a plesiomorphic and Asterothyrium an apomorphic element, the closest relative of the Asterothyriaceae must be searched for near the former and not the latter, as often erroneously done (Vezda & Poelt 1990, Dennetière & Péroni 1999, Lücking 1999). When introducing Gyalideopsis, Vezda (1972) compared it with Gyalidea, from which it was distinguished by branched and anastomosing paraphyses and hyphophores, but the obvious relationship between Gyalidea and Gyalideopsis was eventually obscured by the disintegration of the Asterothyriaceae (Vezda & Poelt 1987, 1990). For example, in the description of Gyalideopsis, the ascus type was given as “... von gleichen Bau wie bei Gyalidea ...” (Vezda 1972: p. 205), but later described as fissitunicate by Vezda & Poelt (1987). This was based on observations made by Hafellner (1984) on Gomphillus “... probably due to the long and thin asci with very thin, needle-shaped ascospores”. In certain Ostropales, the ascus apparatus might appear bitunicate but is not functionally so: “... bitunicate asci are difficult to demonstrate in specimens of filiform-spored fungi ...” (Sherrwood 1977: 27).

Thus, the differences between Gyalidea and Gyalideopsis are exactly as outlined by Vezda (1972). Both genera share the same ascus type and are identical in other features (Table 3). Differences are only seen in the branched and anastomosing paraphysoids and the formation of hyphophores in Gyalideopsis. However, paraphysoids occur in the lateral parts of the hymenium in some Gyalidea species, and species of Gyalideopsis may have almost unbranched paraphyses and lack hyphophores. Therefore, Gyalidea and Gyalideopsis may share a common ancestor, indicating that Asterothyriaceae and Gomphillaceae are closely related families with

| Table 3. Comparison of morphological, anatomical, and ontogenetical features in Gyalidea and Gyalideopsis (based on Vezda 1966). |

Features shared between the genera:  
gyalectoid (often slightly translucent) apothecia  
hamiangiocarpous apothecial ontogeny  
excipulum of branched hyphae embedded in  
gelatinous matrix, rarely  
paraplectenchymatous  
non-amyloid (I-negative) hymenium  
"annelascaceous" ascus with apical ring  
(Gyalidea-type)  
transversely septate to muriform, thin-walled  
ascospores, constricted at septa  
chlorococcoid phycobiont  

Features separating the genera:  
Gyalidea  
true paraphyses  
(unbranched)  
pycnidia (rare)  
Gyalideopsis  
paraphysoids (branched  
and anastomosing)  
hyphophores (common)
parallel evolutionary trends, such as the folijicolous growth and the evolution of immersed-erumpent (paedomorphic?) apothecia.

Members of the Ostropales were excluded from most large-scale phylogenetic studies of the Ascomycota (Gargas et al. 1995, Stenroos & DePriest 1998). Only recently, the monophyly of the order, including representatives of Stictidaceae (Stictis radiata (L.) Pers., Conotrema populorum Gildenstam), Thelotremataceae (Diploschistes ocellatus (Vill.) Norman), and Graphidaceae (Graphis scripta (L.) Ach.), was established by Winka et al. (1998) based on LSU rDNA sequences. This was confirmed by LSU rDNA data, and it was even found that this group should include the Gyalectales (Lutzoni et al. 2001, Lumbsch et al. 2001; Kauff & Lutzoni 2002; and R. Lücking et al. unpubl.). Judging from phenotype data, besides the Gyalectaceae/Coenogoniaceae, there appear to be three lineages within the order in its present circumscription: the largely non-lichenized Stictidaceae/Odontotremataceae, the lichenized Asterothyriaceae/Gomphillaceae, and the lichenized Thelotremataceae/Graphidaceae. Whether all these are natural entities, and whether lichenized clades evolved from non-lichenized ones or viceversa (or both?), remains to be studied and requires more detailed approaches including molecular methods.

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